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Observations on the Prey and Nests of *Podalonia occidentalis* Murray (Hymenoptera: Sphecidae)

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Abstract.—Podalonia occidentalis Murray is evidently a specialist on last instar larvae of tent caterpillars (*Malacosoma* spp.) (Lasiocampidae), as evidenced by records from New Mexico, Nevada, California, Alberta, and numerous records reported here from north central Colorado. Nests are shallow and typical of other *Podalonia* species, but much variation in details of nesting behavior was noted. Four species of miltogrammine flies were reared from nests, the four together causing a 75% destruction of the wasps' eggs at this locality.

It is a pleasure to dedicate this paper to that avid and versatile entomologist E. Gorton Linsley, whose 1956 paper on *Cerceris californica* (with J. W. MacSwain) is a small classic of its kind. Sphecology is the worse for his fascination with wasps' "fuzzy relatives," the bees, and with longhorned beetles and diverse other insects. I spent only a few days with "Gort" in the field, but they were enough to charge my batteries for some time to come.

The present report concerns sphecid wasps of the genus *Podalonia*. Most species of this genus prey on cutworms (Noctuidae), which they exhume from the ground and use to provision a shallow nest dug nearby (reviews in Murray, 1940; Bohart and Menke, 1976; see also O'Brien and Kurczewski, 1982; Steiner, 1983). There are, however, at least two species of this genus that capture hairy caterpillars that live well above ground. The best known of these is *P. valida* (Cresson), which is a specialist on "woolly bears" of the genus *Estigmene* (Arctiidae) (Steiner, 1974, 1975). I have many records from north central Colorado that indicate exclusive use of saltmarsh caterpillars, *E. acrea* (Drury), in this area. A second species, *P. occidentalis* Murray, has been the subject of a brief report by Murray (1940). Near Santa Fe, New Mexico, these wasps were found "working with much effectiveness on the tent caterpillar" in the month of June. Williams (1928) reported *Podalonia violaceipennis* (Lepeletier) preying upon tent caterpillars at 1980 m in the Sierras of California. He found 11 nests in close proximity and believed that all were made by one female. The species of *Podalonia* have often been confused in the past, and it seems quite possible that Williams was dealing with *occidentalis* rather than *violaceipennis*.

There are three previously unpublished records of *P. occidentalis* preying upon *Malacosoma*. R. M. Bohart (personal communication) has collected females carrying tent caterpillars at Sagehen Creek, Nevada, where there was a large population of the wasps in 1974, following an outbreak of tent caterpillars in previous years. M. F. O'Brien has sent me two additional records of *P. occidentalis* based on museum specimens (personal communication). A female in the Canadian National Collections, from Pincher, Alberta, was collected by R. W. Salt on 9 July 1941 with a

Malacosoma larva; and four females in the University of Michigan Museum of Zoology, from Crowley Lake, Mono Co., California, were collected by L. Bezark on 8 June 1976 "carrying tent caterpillars."

The observations reported here were made between 16 and 23 June 1985 and between 12 and 30 June 1986, at three sites 2–5 km apart, all about 23 km west of Livermore, Larimer Co., Colorado, at an elevation of about 2300 m. In this area western tent caterpillars, *Malacosoma californicum* (Packard) (Lasiocampidae) are extremely common, especially on bitterbrush, *Purshia tridentata* (Pursh). The active period of *P. occidentalis* appears to correspond closely with the time when tent caterpillars reach the final instar and leave their tents to feed individually. I did not observe prey capture in the field but several times saw females carrying prey from areas where caterpillars were feeding on *Purshia* bushes. Without exception prey carriage and nest construction occurred during the morning hours, between 0840 and 1115 Mountain Daylight Time. Both males and females were frequent visitors to the flowers of miner's candle, *Cryptantha virgata* (Porter), which blooms in abundance during the active period of the wasps.

The three study sites were all along trails or little-used dirt roads, either in tracks or in bare places along the roadside. In every case there were infested *Purshia* bushes not far away. It was common to see males patrolling these sites, flying back and forth in a weaving pattern 5–15 cm above the ground. Occasionally a male descended upon a female that was active at a nest, but contact was broken off immediately. I saw only one copulation. In this case a female walked along a road with a male astride her, holding her in the neck region with his mandibles. He extruded his genitalia briefly before flying off after about 20 seconds. I did not see the initial union of the pair, which may have occurred many seconds or minutes earlier. R. M. Bohart (personal communication) observed about 40 males forming a struggling ball around a female along a dusty road at Sagehen Creek, Nevada. This occurred during a period of unusual abundance of *Podalonia occidentalis*.

I observed stinging of the prey twice. On 12 June, at 0950, a female was seen carrying a caterpillar along a road. She dropped the prey and disappeared for three minutes; when she returned she stung the prey seven times (even though it appeared already well paralyzed). She mounted the prey obliquely over its back and stung it along the midventral line, beginning at the thorax and moving back slightly each time, covering most of the length of the abdomen. Essentially this same behavior was observed in a terrarium, where a female *Podalonia* had been placed with tent caterpillars.

Females carry their prey forward over the ground, holding it venter up, the wasp grasping the caterpillar with her mandibles on the first or second abdominal segment and straddling it. Since the caterpillars are much longer than the wasp, they extend a considerable distance in front of and behind the wasp. In four instances the wasp was seen to proceed to a plot of more or less bare, friable soil and then deposit her prey while she searched for a place to dig. In one instance a female, with much apparent effort, pulled her prey into a weed 2 cm off the ground. She then walked about and scraped the soil here and there, returning to her prey in 18 minutes and again in 29 minutes, each time moving it slightly. Finally, 33 minutes after entering the site, she started a nest 2.5 m away from the prey. Nest construction required only 10 minutes, and the female then returned to the prey and carried it directly to the edge of the hole. She then entered and pulled the prey in head first. She emerged within a few

seconds and began filling the burrow by scraping in soil from the edge of the hole. Filling was complete in 3.5 minutes, and the female then rested in the shade of a plant and cleaned herself for 3 minutes before flying off.

Similar behavior was observed on three other occasions, although in each case the prey was left on the ground in the shadow of plants or within a grass clump. In two instances, a wasp was seen to leave a caterpillar under a plant and not return for several hours. In one case the caterpillar was eventually carried off by several ants (*Formica* sp.).

In contrast, there were three other occasions when it was clear that the wasp prepared her nest first, leaving it open and provisioning it much later. In each case a female was seen completing a nest in the morning, but the nest was not provisioned and closed until the morning of the following day. Two of these instances occurred late in the active season (21–22 June) when most tent caterpillars had spun their cocoons. In one case the caterpillar was undersized and bore several eggs of Tachinidae; evidently it had been unable to attain full size and pupate. Thus it appears that when females are unable to obtain prey during a morning hunting period, they proceed to dig a nest, leaving it open and filling it later. I found two nests that were never filled.

Nests are shallow and are dug with rapid thrusts of the fore legs, small pebbles being pulled out with the mandibles. The burrow is about 1 cm in diameter and is oblique, terminating in a horizontal cell about 2.5 cm in length at a depth of from 2 to 6 cm (mean 3.9 cm, n = 14). Since the cell is shorter than the prey, the latter is coiled in a broadly C-shaped posture, lying on its side. The egg measures 2.5 mm in length and is laid vertically on the uppermost side of the abdomen, its anterior end attached firmly to the prey, the posterior and extending ventrally free from the prey. Of 11 eggs recorded, seven were attached at an intersegmental membrane, three between A2 and A3, two between A3 and A4, and two between A4 and A5. Four others were attached toward the middle of the segment, three on A3 and one on A4.

Following oviposition, the female fills the burrow rapidly from soil at the periphery of the entrance. In five of nine closures observed, much of the soil was taken from a shallow quarry close beside the entrance; in three of these cases there were two such quarries. The quarries varied from 0.5 to 2.0 cm in depth and from 2 to 4 cm in distance from the entrance. Presumably these quarries are homologous to the accessory burrows that have been described in a variety of digger wasps (Evans, 1966). A portion of the mound at the nest entrance is usually left intact, and nests (especially those with quarries) can sometimes be spotted in the absence of the wasp. Closures are not always completed level with the soil surface; in one case the top 1.5 cm of the burrow was left unfilled.

The egg hatches in about two days and full larval development requires eight to 10 days. However, of 12 nests in which the egg was recovered, nine contained maggots that quickly destroyed the egg and later the prey. Four different species of Miltogramminae (Sarcophagidae) were involved, maggots numbering two to 12 per nest. In order of abundance the flies were:

Hilarella hilarella (Zetterstedt), 14 flies from 4 nests
Sphenometopa sp. nr. *nebulosa* (Coquillett), 10 flies from 3 nests
Taxigramma heteroneura (Meigen), 2 flies from 1 nest
Senotainia trilineata (Wulp), 2 flies from 1 nest

Flies emerged from 22 to 32 days following the date of larviposition. Oddly, I rarely saw these flies in the field; only on one occasion did I see a satellite fly perched on a stone 15 cm from a female that was digging a nest. Others have noted that *Hilarella* is an especially prevalent parasite of species of *Podalonia* (Murray, 1940; O'Brien, 1983).

Podalonia occidentalis appears to be a specialist on *Malacosoma,* and the wasps disappear from the field when the tent caterpillars have pupated. On one occasion I placed a female in a terrarium with several *Malacosoma* larvae; she stung one of them (as described above) but failed to lay an egg or bury the prey. On a second occasion I placed a *Podalonia* female in a terrarium with two *Malacosoma,* two unidentified "woolly bears" (Arctiidae), and two cutworms (Noctuidae). She stung one of the *Malacosoma* but failed to attack the others. These experiments are far from conclusive, but so far as they go they do tend to support evidence from the field, where 17 prey records were obtained, all involving *M. californicum.*

Discussion

Despite the host specificity of *Podalonia occidentalis,* many aspects of its behavior seem unusually variable. Both prey and nests were sometimes abandoned; nests were sometimes incompletely filled; some nests were filled with quarries (either one or two) and others lacked quarries; egg position varied considerably. The most striking variation was in the prey-nest or nest-prey dichotomy. This behavioral difference is often considered a fundamental one, most *Podalonia* (and many other more generalized wasps) taking prey before they make a nest (for reviews see Evans and West-Eberhard, 1970; Iwata, 1976). However, such variation has been reported in at least two other species of *Podalonia* (Myartseva, 1963 [cited in Bohart and Menke, 1976]; Tsuneki, 1968). *P. valida* females regularly dig the nest before obtaining prey (Steiner, 1975; personal observations). *P. valida* is unusual in that females make a series of nests in a restricted territory that is defended against intrusion by other females. There was evidence that *P. occidentalis* females return again and again to the same general area to nest, but nests were not closely clumped and there was no evidence of territorial behavior. *Podalonia* appears to be a genus in transition with respect to whether the prey is taken before nest building (as it is in the genus *Prionyx,* a member of the same subfamily) or whether the nest is dug first (as it is in the closely related genus *Ammophila*).

The incidence of parasitism by miltogrammine flies (75%) is possibly the highest ever recorded for a digger wasp. Since *P. occidentalis* nests earlier in the season than most digger wasps, its inability to avoid the attacks of miltogrammines may permit these flies to build up populations that are able to exploit species that nest later in the summer (species of *Ammophila, Philanthus,* and other genera, in fact occurred in these same study sites). The great abundance of tent caterpillars might seem to compensate for the high incidence of parasitism, but in fact I have no evidence that females ever provision more than one nest a day, and they are restricted to the brief period when tent caterpillars are in the final instar. The impact of *P. occidentalis* on the natural control of these pests appeared negligible in the study area.

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